

A REVISION OF THE ASIATIC GENUS LINOSTOMA (THYMELAEACEAE)

LORIN I. NEVLING, JR.

THE SUBTRIBE LINOSTOMATINAE of the Thymelaeaceae is composed of three closely related genera which have been combined taxonomically in various ways in the past. Previous treatments of these genera have not been inclusive, and, therefore, a preliminary survey to establish generic limits has resulted in considerable realignment of the species. Two of the genera, *Linostoma* Wall. ex Endl. and *Enkleia* Griff., are restricted to the area from India to Indochina, Malay Peninsula, and adjacent islands, while the third, *Lophostoma* Meissn., is restricted to the Amazon basin. Numerous examples of a disjunction between southeastern Asiatic and southeastern North American groups have been studied and reported but an Asian-Amazonian disjunction is unusual. For this reason an attempt will be made to define as precisely as possible the interrelationships of *Linostoma*, *Enkleia* and *Lophostoma*. In order to pursue these interrelationships it is believed essential to revise each of the genera concerned prior to generalizing about the subtribe as a whole. Accordingly, this revision of *Linostoma* is the first of a contemplated series.

SPECIAL MORPHOLOGY

Some of the more interesting morphological features found within the genus *Linostoma* during the course of this taxonomic investigation are presented in the following discussion. A few of these features have not been reported previously for the genus, and others are emphasized to indicate problems requiring additional investigation. Also included are several anatomical elements which have been employed previously as taxonomic characters and which I feel demand at least a summary review. Finally, additional information can be found in the body of the descriptions and in the discussion following each species.

It must be stressed that the number of specimens examined (indeed available) was far too few to obtain any but the very roughest type of information. A more thorough investigation which would include a study of the variation in individual plants in the field and under experimental conditions is necessary as the first step to an understanding of the variation exemplified in the herbarium specimens. However, even this brief study gives minor support to the taxonomic delimitations presented in this revision.

The leaves and flowers were prepared for study by gentle heating in water plus a commercial detergent until softened and then were cleared with a 5% solution of sodium hydroxide (Foster, 1950). The hydroxide

treatment often left the specimens in a too softened condition. This was remedied by treatment with chloral hydrate, which tends to harden the tissue and at the same time accounts for some additional clearing. In practically all instances it was necessary to bleach the specimens in 50% "Clorox" to obtain final clarity. The time necessary for the clearing processes varied widely from specimen to specimen.

The cleared leaves were stained with a 1% safranin solution in 95% ethyl alcohol for venation studies or with 5% ferric chloride and tannic acid in 70% ethyl alcohol for the study of cell types. The latter staining was particularly useful in studying the stomata. All specimens were dehydrated appropriately and mounted in Gum Damar or "Diaphane." As in the clearing processes, the staining times varied quite widely.

Cleared flowers were studied both unstained and stained; when stained, a 1% solution of safranin in 95% ethyl alcohol was used. I personally feel that the stained specimens are more useful, particularly when the finer vascularization is being studied. The stained flowers were dehydrated and mounted in Gum Damar.

Leaf cross sections and petioles were prepared for study by boiling in water or by clearing as in the procedure outlined above. They were embedded in paraffin through a tertiary butyl alcohol series and sectioned. A safranin-fast green staining schedule was followed.

In addition, free-hand sections stained with potassium iodide and sulphuric acid, as well as with phloroglucin and hydrochloric acid (Foster 1950) were later found to be useful in determining the degree of lignification of certain tissues. This technique has been employed with stems, petioles, leaves and bracts.

Vegetative Morphology. The vegetative axis is monopodial, but the precocious development of axillary buds often obscures this nature. Several types of branching usually can be observed within any single relatively large collection. The simplest pattern is one in which dichotomous branching, with equal development of both axes, appears to have taken place. This type is the result of the destruction of the apical bud followed by development of the opposite axillary buds. An aborted terminal bud often may be observed in the fork of the dichotomy but it is gradually obscured with time. A second type of branching, also appearing to be dichotomous but unequally so, is the result of the continued growth of the main axis accompanied by the development of one of the axillary buds of the subtending node. The most striking pattern, however, is in the form of a trichotomy. This pattern is formed by the continued growth of the main axis accompanied by the simultaneous development of both axillary buds of the subtending node. The members of the trichotomy may be developed equally or unequally, and, in addition, the lateral axes may be slightly subopposite, depending on the exact position of the axillary buds.

In a few instances, the branching patterns described above are not clear-cut because the leaves subtending the developing axillary buds some-

times do not appear to be present. These leaves are then borne on the developing axillary branch beyond the point of external furcation. They are usually near the division and are unpaired, in contrast to the leaves of the normal axis. The trace which supplies these leaves is initiated below the external furcation as is the trace of the axillary bud. Immediately below the external furcation the division of leaf and axillary bud traces is not yet complete. For some unknown reason the leaf is then "carried out" onto the developing axillary branch which it actually subtends. This phenomenon is more prevalent in the inflorescence and is further discussed there.

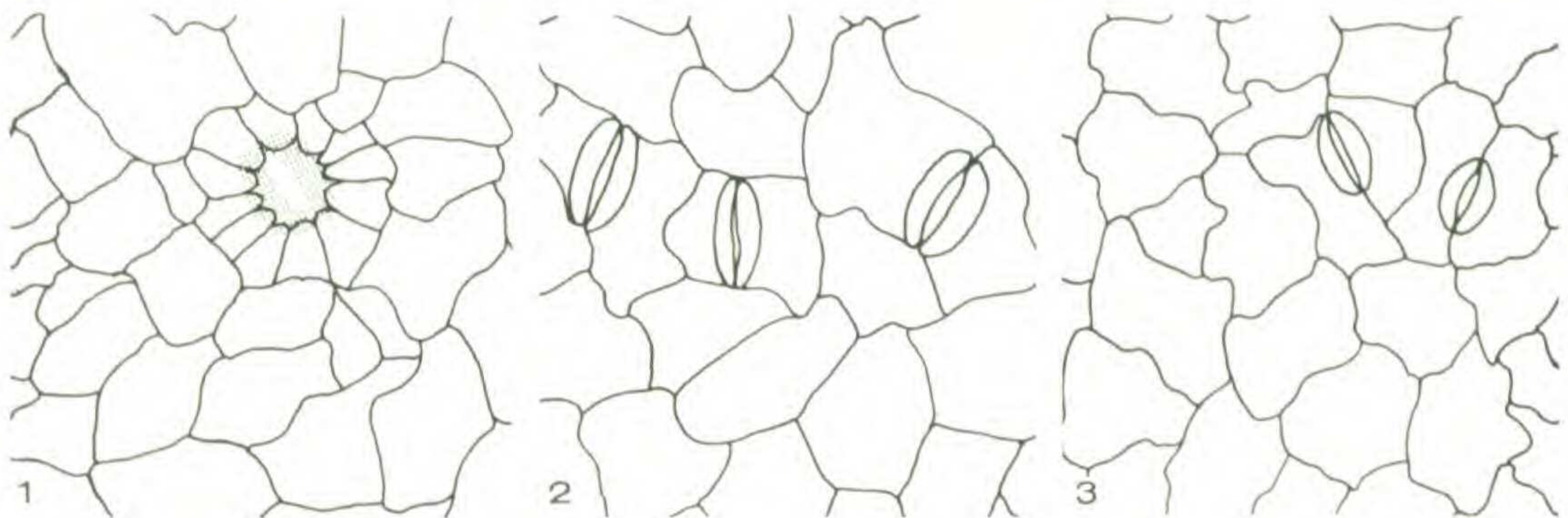
The axillary branches themselves are of interest in that they may be ascending or become weakly to strongly uncinatate, facilitating climbing or scrambling. The "hooks" are similar in appearance to those found in species of *Cardiospermum* (Sapindaceae) or in *Schefflera caudatifolia* Merrill (Araliaceae). There are reports (Metcalf & Chalk, 1950) based on stelar anomalies indicating the possible origin of genera with shrubby or treelike habits from lianallike ancestors. It is because of the development of the uncinatate branches that the habit of individual species appears to be so diverse. I suspect that the plants of *Linostoma* are erect shrubs or trees which are not above scrambling if the opportunity presents itself.

The presence of an extraxylary fiber sheath surrounding the stele often is used as a diagnostic characteristic of the family. These fibers are often employed as twine in various parts of the world. They have relatively thick walls of cellulose and, in this genus, may become slightly lignified after a number of years. The lack of strong lignification of the fibers may contribute in part to the flexibility of the stems.

The structure of the leaf was investigated because of the widespread use of the venation pattern as a means of distinguishing between *Linostoma* and *Enkleia*. The leaves are dorsiventral. The upper epidermis, covered by a rather thick cuticle, is composed of relatively large tabular cells in *L. persimile* and *L. pauciflorum* and is devoid of stomata. A hypodermis of large, thin-walled cells is also found in these two species. In *L. decandrum* a single epidermal layer, comparable to the double layer of the other species, is found. The palisade layer immediately below is compact and composed of more or less isodiametric cells which are at most only a fifth the size of the epidermal cells. This palisade appears to be three or four cells thick. Within this layer or the one following, occur some large, thin-walled cells which contain druse-like crystals. These crystals are most prevalent in *L. decandrum*. The spongy parenchyma layer below the palisade is extremely loose, with very large air spaces. The cells composing this layer are comparatively large and generally are branched. The lower epidermis is composed of tabular cells which, in the case of *L. pauciflorum*, are conspicuously bullate on the outer periclinal wall. This peculiar papillation of the lower epidermis gives a characteristic farinose appearance to the lower leaf surface when viewed under low magnification. The cells of the lower epidermis, which is in-

errupted by numerous stomata, are consistently smaller than those of the upper epidermis.

In *Linostoma persimile* and *L. pauciflorum* the stomata are similar, and it is impossible to distinguish these two species on the basis of stomatal type or size (TEXT FIG. I, 2, 3). These stomata are of the ranunculaceous type (accessory cells morphologically similar to the surrounding epidermal cells). This stomatal type has not been reported previously for the genus, although it is well known in other genera of the family. The guard cells are borne in the same plane as the epidermal cells.



TEXT FIG. I. Camera lucida drawings of the lower leaf epidermis of *Linostoma*. 1, *L. decandrum* (Parry 410); 2, *L. persimile* (Garrett 1397); 3, *L. pauciflorum* (Kerr 11820A). Stippling indicates stoma on different plane from surrounding cells.

The stomatal condition is more complex in *Linostoma decandrum*. Instead of a pair of accessory cells as in the previous species, there is a cluster of small cells completely surrounding the stoma. Each cell is awl-shaped and bends slightly over and beyond the guard cells so that an urceolate structure is formed. The guard cells are situated at the base of this pit and are, in addition, borne in a plane above that of the lower epidermis (TEXT FIG. I, 1; also Solereder *Fig. 174, B, C* and repeated in Metcalfe and Chalk, *Fig. 284, B, E*).

The pinnate venation is essentially similar in all species of the genus. The primary lateral veins are very numerous and close to each other (several millimeters apart at most) and are more or less straight, parallel, and simple, but sometimes dichotomize. Each vein is subtended by an extraxylary fiber-sheath which is often more extensive than the vein which it supports. Each primary vein terminates in, and contributes to, a submarginal vein. The submarginal vein, with accompanying fibers, is often better developed than the contributing lateral veins (except in *L. persimile*). Its proximity to the margin varies slightly among the species.

The secondary veins, after departing from the primary veins, run more or less parallel to them. The very fine appearance of the venation is due to this parallel orientation of veins and veinlets. The veinlets are also subtended by the extraxylary fibers. These fibers react strongly with potassium iodide and sulphuric acid to give a deep blue color but do not give a color reaction to phloroglucin and hydrochloric acid. On this basis

it appears that they are composed of cellulose and are not lignified. The fiber sheath extends almost to the end of the veinlet where it is often replaced by variously shaped sclereids. In *Linostoma persimile* these sclereids do not extend to the vein-ending, but in both *L. decandrum* and *L. pauciflorum* they extend either to the vein-endings or slightly beyond them (see TEXT FIG. II).

Cross sections of the petiole were studied to check information in Metcalfe and Chalk (1950) indicating the presence of intraxylary phloem in petioles of *Lophostoma* and *Enkleia* but not *Linostoma*. In all species of *Linostoma* the xylem, at mid-petiole, is arc shaped and often is interrupted by rays a single cell broad. In *L. decandrum* and *L. pauciflorum* it appears that phloem can be found both above and below the xylem-arc, thus indicating the presence of intraxylary phloem within the genus, contrary to previous reports. In *L. persimile* the phloem is found only below the xylem-arc. At best this seems to be only an academic point and appears to lack taxonomic significance.

The fibers which usually accompany the vascular bundles either are poorly differentiated in the petioles or are lacking altogether. When present, they have a negative color reaction with phloroglucin and hydrochloric acid. However, they stain very dark blue with potassium iodide and sulphuric acid indicating the cellulosic nature of the cell walls.

Reproductive Morphology. At the time of the initiation of the flowering response the vegetative pattern in the terminal portion of the shoot becomes modified. The changes which take place in the external morphology of the shoot at this time possibly are controlled by the same physiological forces which cause the induction of the flowering response.

The same basic terminology which I applied to the inflorescence of *Daphnopsis* in a previous paper (1959, pp. 262, 263) is used here. The inflorescence is considered as being composed of the basic units of primary peduncle, rachis, secondary peduncles and flowers with their pedicels. There are a few additional features in the inflorescence of *Linostoma* not found in *Daphnopsis*, and these are discussed below.

The flowering shoot is composed of many inflorescences, the sum of which appears to form a single large and highly branched, terminal inflorescence. The flowering response destroys the apical dominance of the stem apex, and the axillary buds of several subtending nodes begin development. This complex change must take place during the initiation of the affected parts and prior to their subsequent elongation. The resulting precocious development of the axillary branches is responsible for the decidedly peculiar appearance of the inflorescence. The main stem axis appears to trifurcate (see also discussion of branching patterns) without good cause, i.e., without subtending leaves. This pattern is due to the initiation of the leaf traces and the axillary bud traces shortly below the external furcation, followed by rapid elongation to the extent that the leaf is "carried out" onto the axillary shoot which it actually subtends. The external relationships of vegetative shoot, axillary branches and

leaves are obscured. The developing axillary shoots may undergo several such divisions until a large paniculiform structure is developed. As a result, the primary peduncle often bears near its base the reduced, displaced leaf of the subtending node. This displaced leaf is homologous to the bract found on the compound inflorescences of some species of *Daphnopsis* (especially *D. americana*).

At the apex of the primary peduncle is borne a single small bracteole, which is usually caducous but occasionally persistent. This structure is further discussed following *L. pauciflorum*.

In addition, the primary peduncle bears a pair of bracts. These bracts are opposite to alternate and are borne at or below the middle of the primary peduncle (*Linostoma decandrum* and *L. persimile*), or from the middle to the summit (*L. pauciflorum*). These bracts appear to be expanded fully, or nearly so, by the time the flowers attain anthesis. This contrasts with the situation in *Enkleia* in which the expansion of bracts is delayed until shortly after anthesis. The function of these bracts is uncertain, although Domke has used the very appropriate term "Flugbrakteen" to describe them and Ridley has included this genus in his book (1930) on plant dispersal under the heading "Bract Wings." Speaking of the bracts in *Linostoma* he says (p. 92), "They become pale and papery when the fruit is ripe, and are detached, adhering to the fruit, so as to be blown away separately." He attributes the small size of the plants of *L. persimile* to the drupe being too heavy to be borne away by the bracts, whereas, in *L. decandrum* and *L. pauciflorum* the drupe is light enough to be easily drifted. Finally, he says (p. 93) "Here the reduction of the number of fruit produced on the spray, and the persistence of the terminal pair of leaves, has converted a bird-dispersed plant into a wind-dispersed one, and has allowed the plant to be successful in climbing to the top of the forest." Theoretically, I disagree with Ridley because it appears, on the basis of herbarium material, that all separations of fruit plus peduncle with bracts are mechanical accidents. In these cases the peduncle at the point of separation is irregularly broken and does not seem to be as easily separated as at the articulation zone between pedicel and secondary peduncle. Ridley has seen the plants in nature and what appears to be theoretically improbable may occur in actuality.

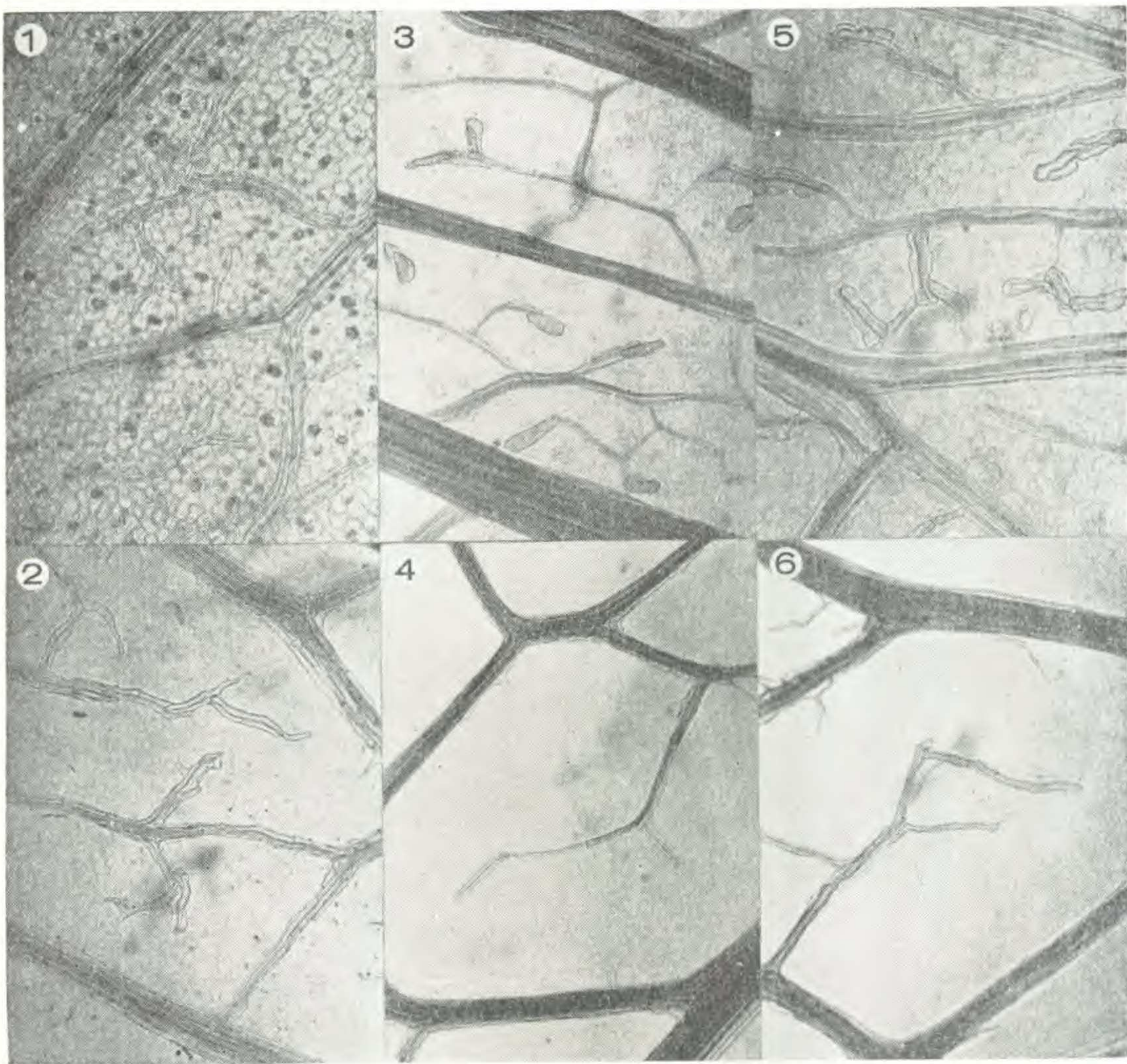
The shape and structure of the bracts are in several respects different from those of the foliage leaves. The bracts vary from ovate to oblanceolate but are of a shape and size usually quite dissimilar from that of the leaves. In addition, they are much thinner than the leaves and are distinguished further by their white to cream color. In spite of their extreme thinness, the bracts retain the same morphological components (i.e., epidermis, palisade and spongy parenchyma) and in approximately the same ratio as the leaves.

Another, and perhaps more striking, characteristic of the bracts is the relative spaciousness of the venation. The venation pattern is, in fact, more like that which one would expect to find in leaves, i.e., more reticulate. The number of primary veins is greatly reduced from the number

found in leaves. In addition, the number of secondary, and particularly smaller, veins is much lower. The lack of development of the smaller veins accounts for the appearance of spaciousness of the venation. As in the leaf, a submarginal vein is present in all species.

The extraxylary fiber sheath associated with the veins differs from that of the leaves in one striking aspect. In contrast to the leaf, the sheath supporting the minor veins is not constituted entirely of fibers but often has an outer layer composed of relatively short sclereids. These sclereids are irregularly shaped, with at least one surface noticeably enated. This characteristic allows microscopic identification of leaves and bracts (see TEXT FIG. II).

The fiber sheath reacts to the lignification and cellulosic tests in the same way as in the leaves. The color reaction indicating cellulosic walls lacking lignification is less intense than in the leaves. In like manner, the color reaction indicating lignified xylary elements also is much less



TEXT FIG. II. Photomicrographs of fine venation of leaves and bracts of *Linostoma*. 1, *L. decandrum*, leaf (Wallich 4203); 2, *L. decandrum*, bract (Wallich 4203); 3, *L. persimile*, leaf (Garrett 1436); 4, *L. persimile*, bract (Garrett 1436); 5, *L. pauciflorum*, leaf (Hallier B.2261); 6, *L. pauciflorum*, bract (Hallier B.2261). Note numerous crystals in leaf of *L. decandrum*.

intense, and it seems that the tissues of the bracts are developed much less than those of the mature leaves.

The flowers are arranged on the rachis in an indeterminate fashion (the lowermost flower blooming first). The flower clusters are umbelliform to subracemiform, depending on the relative length of the rachis. I suspect (without substantiating evidence) that the condensation of the rachis and the resulting clustering of flowers is due to selective pressures in favor of the formation of a pseudanthemum.

The flowers are bisexual, regular, pentamerous, perigynous, and pedicellate. They are probably conspicuous at anthesis by their coloration and by the presence of the light-colored subtending bracts.

The terminology applied to the parts of the thymelaeaceous flower has varied with the individual author's personal inclinations. Accordingly, I am retaining the same terminology that I used in *Daphnopsis* (Nevling, 1959) and that for the same reasons. Further gross morphological information, beyond that presented in the following discussion, concerning the flower may be found in the specific descriptions.

The calyx tube is appendicular in origin, that is, composed of the fused bases of calyx, corolla, and androecial members. It is always tubular, although the exact shape is variable, and surrounds the superior ovary. The exterior is glabrous, while the interior varies from entirely villous to glabrous. The trichomes are exclusively unicellular and unbranched.

The tube is vascularized by ten distinct veins which are marked externally by conspicuous ridges. Near the orifice the traces to the androecium depart, one to each stamen. Above the departure of androecial traces the vascular pattern becomes exceedingly obscure due to the proliferation of traces and to the overlying pubescence. I am not satisfied with my results in this critical area of the calyx tube.

The size and shape of the five calyx lobes vary among the species. The position of the lobes at anthesis is a more important taxonomic character. In *Linostoma decandrum* they are strongly reflexed, in *L. pauciflorum* they are spreading, and in *L. persimile* they are erect to slightly spreading. In all species the lobes are vascularized by three main veins. The lateral veins often proliferate at the orifice, and all send off numerous branches which often anastomose, particularly towards the lobe apex. Extraxylary fibers are present even on these small veins.

The ten petals are inserted in pairs at the orifice of the calyx tube in an alternisepalous position just above the outer staminal whorl. Two closely related petal types are found in the genus: (1) in *Linostoma decandrum* the clavate petals are united at their bases by an inconspicuous annulus; (2) in *L. pauciflorum* and *L. persimile* the clavate or liguliform petals are free at their bases. In all species the petals are glabrous and erect.

The shape of the petal apex has been found to be a useful taxonomic character. It is dependent on differential growth patterns (particularly differential elongation of separate whorls). The elongation patterns are reflected in the relative position of petals, anthers and stigma in the

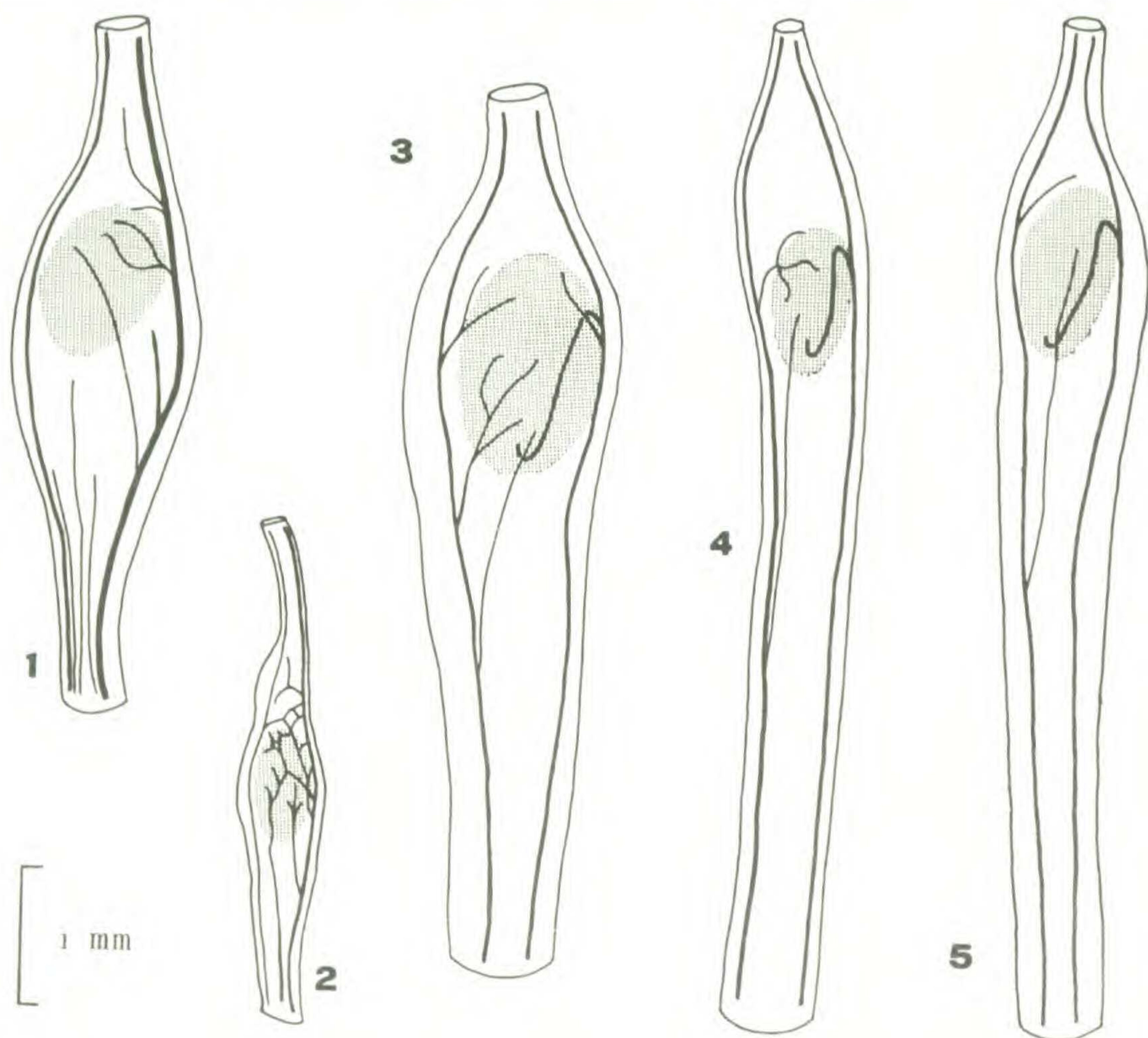
mature flower. In this respect two exsertion orders are found: (1) stigma, anthers and petals in *Linostoma decandrum* and *L. pauciflorum* (petal apex obtuse or irregular); (2) petals, stigma and anthers in *L. persimile* (petal apex acute).

The distortion of the petal apex in *Linostoma decandrum* occurs as the pairs of petals develop in the alternisepalous position. In the bud their apices become appressed to the base of the developing alternisepalous anther. Elongation of the petal apparently occurs at a slightly faster rate than that of the developing staminal filament, with the result that each petal apex clasps one of the lower lateral margins of the alternisepalous anther, thus deforming the petal apex. Although the filaments subsequently elongate and the petals undergo further elongation, the apices never recover from the initial contact with the anther. As a result, the petal apex is often cup-shaped or truncated with one lateral margin (that toward the calyx lobe) noticeably longer than the other. This same situation is found in *L. pauciflorum* to a much lesser degree, with the result that the petal apices are never as strikingly deformed as in *L. decandrum*. The acute petal apex of *L. persimile* is due to the lack of interference of petal elongation by the androecium. It is impossible to say whether this condition is advanced or primitive in relationship to that found in *L. decandrum* and *L. pauciflorum*.

In *Linostoma persimile* and *L. decandrum* vascular tissue is lacking in the petals. This is really quite surprising, for petal length in these species is 3.5 and 3.5–6 mm. respectively. It is difficult to understand why fleshy structures of this size require no vascularization. In *L. decandrum* the petals are inserted between the midrib supplying the calyx lobe and the lateral veins, which at this level have already divided several times. It does not appear to be associated more intimately with the lateral veins than with the midrib as might be expected.

The petals of *Linostoma pauciflorum* are vascularized by a single trace. I have observed an exception in one petal in which the trace divided near the base and two well-developed traces were formed. I have been unable to determine the connection of the petal trace with a calyx tube trace. The trace is usually 5–10 tracheids in diameter, and these tracheids have annular to helical thickenings. Toward the petal apex the tracheids become noticeably shorter and the trace finally ends blindly.

The androecium consists of ten stamens inserted on the calyx tube just below the petals. The stamens are inserted either in two whorls (*L. persimile* and *L. pauciflorum*) or in a single whorl (*L. decandrum*). The five stamens of the upper whorl are in the antisepalous position, while those of the lower whorl are alternisepalous. The single whorl of *L. decandrum* is in reality two closely intermeshed whorls, for the traces supplying the alternisepalous stamens depart from the lateral commissural calyx traces (in respect to the position of these in the calyx lobe) some distance below those of the antisepalous stamens. The traces supplying the antisepalous stamens are continuous with those of the median calyx traces.



TEXT FIG. III. Camera lucida drawings of vascularization of stipe and ovary of *Linostoma*. 1, *L. decandrum* (Parkinson 316); 2, *L. persimile* (Garrett 1436); 3-5, *L. pauciflorum* (Ridley 1868, Hallier B.2261, Haviland 1759). Stippled portion is the approximate area occupied by the ovule; all vascular bundles, with the exception of the hook-shaped ovular trace in figs. 3-5, are in the ovary wall; only the bundles in the ovary wall facing the viewer are represented.

The filaments are filiform, and those of the antisepalous stamens are usually longer than those of the alternisepalous ones. They are glabrous, except in a single anomalous flower in which they are hispid. Vascularization is by a single vascular bundle which either ends blindly somewhat below the connective tissue or enters only the lower half.

The anthers are exserted, except for those in the alternisepalous whorl of *Linostoma persimile*. They are 4-lobed and 4-loculed in cross section. Dehiscence is longitudinal. The connective is basally inflated in *L. pauciflorum*, and to a lesser degree in *L. decandrum*, so that the pollen sacs are displaced to its lateral margins. In *L. persimile* there is no basal inflation but the connective is produced beyond the pollen sacs.

The pollen of the three species is, for all practical purposes, uniform. It is polyporate and highly sculptured. The grains vary between 40 and 60 micra in diameter, and, although an insufficient number have been

measured, it appears that those of *Linostoma persimile* are the smallest and those of *L. pauciflorum* are the largest.

The disc is borne at the base of the calyx tube and closely surrounds the stipe supporting the ovary; in many previous descriptions the disc has been considered to be absent in the genus. It consists of irregular lobes which are free or connate and sometimes adnate to the calyx tube. The number of lobes is extremely variable within flowers of the same inflorescence and therefore is of little taxonomic consequence. Externally the disc appears fleshy and is glabrous, except in *Linostoma decandrum* in which it may support a few trichomes. Since I have had little success in clearing the disc, which scarcely attains 0.5 mm. in height, I have been unable to determine the vascularization, if any.

The gynoecium is composed of a single pistil, presumably of the pseudomonomeric type, i.e., one fertile and one sterile carpel. It is borne on a stipe (gynophore) which varies in length among the species. In the specific descriptions in the taxonomic treatment the length of stipe and ovary are combined because of the gradual transition between them.

The ovary is superior, ellipsoid to obovoid, and unilocular. It is usually densely sericeous, although occasionally sparsely so in *Linostoma pauciflorum*. The trichomes are unicellular, erect, and quite shiny (at least in herbarium specimens). The pattern of vascular supply to the ovary seems quite distinct among the species (see TEXT FIG. III). *Linostoma pauciflorum* is immediately distinguishable by the well-developed ovular trace (further discussed under the species), the presence of only two traces at the base of the stipe, and few lateral traces. *Linostoma persimile* can be distinguished from *L. decandrum* by the more reticulate secondary venation arising from the main veins. The apparent lack of an ovular trace in the last two mentioned species is curious and requires further investigation. In all species the single, anatropous, two-integumented ovule is semipendulous from the upper locule wall.

The style is borne terminally, although it sometimes appears to be eccentric, in which event the trichomes must be removed before its true position can be seen. It is filiform and is vascularized by two relatively large traces which stand opposite each other. The style is generally glabrous, except in a few specimens of *Linostoma pauciflorum* where a few trichomes can be found. The stigma is capitate or mammiform. (See also discussion following *L. persimile*.)

The flowers of all three species are pedicellate. The junction of pedicel and secondary peduncle is clearly marked by an articulation. In the area of articulation parenchyma cells may be formed at the expense of other tissues. A longitudinal section through the point of articulation in *Linostoma decandrum* has been figured by Leandri (Fig. 23, 3,4. 1930).

In general, the fruits are preserved very poorly and I do not feel qualified to comment upon them at this time. The longitudinally ruptured calyx tube is persistent in *Linostoma decandrum* and can be seen at the base of the fruit. In *L. persimile* and *L. pauciflorum* the calyx tube is accrescent and surrounds the fruit.

GEOGRAPHY

The three species have a composite range extending from India to Indochina, the Malay Peninsula, and the island of Borneo. The distribution is not complicated because of the small number of species. Distributions of the individual species have been plotted on MAP I, which is a part of one of Goode's Series of Base Maps published by the University of Chicago Press. The symbols indicate places of collection only and are in no way indicative of the relative frequency of the plants.

At the present time too little is known of the ecological situations in which the plants grow to give any rational discussion but in only one species, *Linostoma decandrum*, does the distribution appear to be unusual. The disjunction shown by this species is, in all probability, a real one with a lack of suitable habitats between the two areas. There seems to be no morphological basis for the erection of any infraspecific categories in this case.

MATERIALS

This revision is based on specimens from the following herbaria, the abbreviations for which are taken from Lanjouw & Stafleu, *Index Herbariorum*, Part I, Ed. 4 (Regnum Vegetabile 15. 1959).

A	Arnold Arboretum of Harvard University, Cambridge
BM	British Museum, London
C	Botanical Museum and Herbarium, Copenhagen
G	Conservatoire et Jardin botaniques, Genève
GH	Gray Herbarium of Harvard University, Cambridge
K	Herbarium, Royal Botanic Gardens, Kew
L	Rijksherbarium, Leiden
M	Botanische Staatssammlung, München
P	Muséum National d'Histoire Naturelle, Paris
U	Botanical Museum and Herbarium, Utrecht
US	U. S. National Museum, Smithsonian Institution, Washington
W	Naturhistorisches Museum, Wien

I wish to take this opportunity to thank the directors and curators of the above institutions for the many courtesies extended to me. This revision would not be possible without their co-operation. I also wish to thank my colleagues of the Arnold Arboretum and Gray Herbarium for helpful suggestions, technical assistance, and constant encouragement.

TAXONOMY

Linostoma Wall. ex Endl. Gen. 331. 1837 (TYPE: *L. decandrum* (Roxb.) Wall. ex Endl.).

Linostoma Wall. Cat. n. 4203. 1831, sine descript.

Linostoma sect. *Eulinostoma* Meissn. in Mart. Fl. Bras. 5(1): 72. 1855 (TYPE: *L. decandrum* (Roxb.) Wall. ex. Endl.).

Linostoma subg. *Nectandra* Kurz, Jour. As. Soc. Bengal 39(2): 83. 1870
(TYPE: *L. decandrum* (Roxb.) Wall. ex. Endl.).

Trees, shrubs or lianas, often scrambling, the stem monopodial, although frequently dichotomizing or trichotomizing, the axillary branches sometimes modified for climbing, the bark containing many fibers, becoming rugose with drying. Leaves opposite (or sometimes approximate) to alternate, simple, pinnately veined, entire, petiolate, estipulate. Inflorescences borne from the terminal portions of young stems, subracemiform, umbelliform, or rarely the flowers solitary, the primary peduncle bearing a pair of bracts and a single bracteole. Flowers bisexual, pentamerous, perigynous; calyx tube urceolate, ellipsoid or tubular, nonarticulated, ribbed, red, yellow, greenish white or white, glabrous without, glabrous or variously pubescent within; calyx lobes 5, subequal, quincuncial, erect to reflexed at anthesis; petals 10, ligulate to clavate, sometimes with a minute annulus at the base, glabrous; stamens 10, inserted in 1 or 2 whorls, the upper whorl antisepalous, the lower whorl alternisepalous, the anthers filamented, basifixed, longitudinally dehiscent, the connective sometimes produced beyond the pollen sacs or inflated; disc of irregular lobes, sometimes basally connate, sometimes adnate to the calyx tube; gynoecium single, pseudomonomeric, superior, variously stipitate, unilocular with a single anatropous ovule, the style terminal, the stigma capitate or mammi-form. Fruit drupaceous, the calyx tube sometimes persistent or accrescent.

KEY TO THE SPECIES

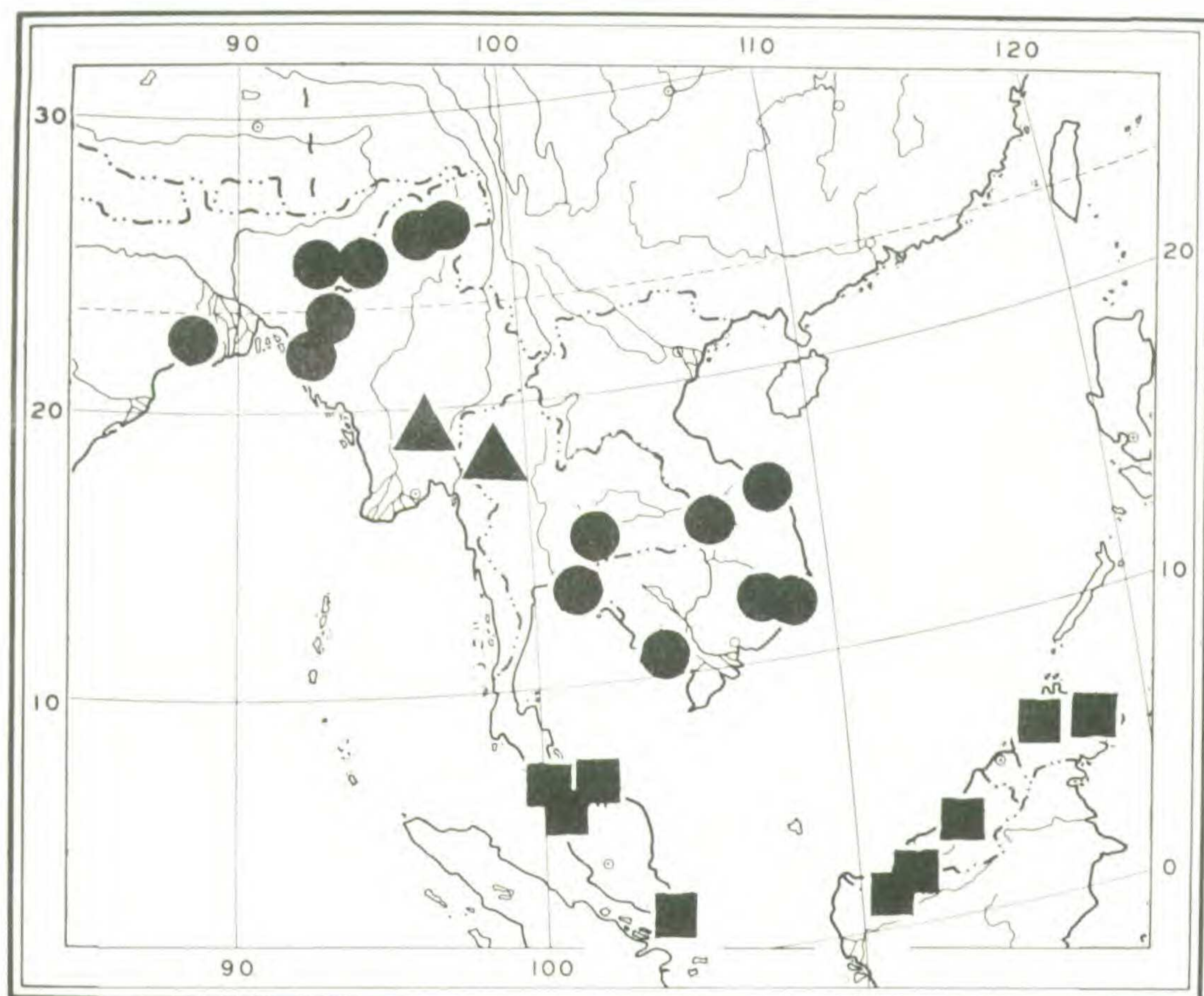
- a. Leaves to 10 cm. long, thick-coriaceous, the apex acute, acuminate or subcaudate; inflorescences 3–12-flowered; calyx tube villous within; calyx lobes generally as long as or longer than the tube, strongly reflexed; calyx persistent but not accrescent in fruit. 1. *L. decandrum*.
- a. Leaves to 5 cm. long, thin-coriaceous, the apex mucronulate and acute, obtuse, truncate or retuse; inflorescences 1–6-flowered; calyx tube villous or glabrous within; calyx lobes at most half as long as the tube, erect or spreading; calyx accrescent in fruit.
 - b. Bracts subopposite, borne at the middle of the primary peduncle or below; calyx lobes erect; petals exerted beyond the stigma and anthers; connective produced beyond the pollen sacs but never inflated; style 6–7.5 mm. long. 2. *L. persimile*.
 - b. Bracts opposite to alternate, at least one of the pair borne near the summit of the primary peduncle; calyx lobes spreading; stigma and anthers exerted beyond the petals; connective inflated so as to separate the pollen sacs at least basally but never produced beyond the pollen sacs; style 6–20 mm. long. 3. *L. pauciflorum*.

1. *Linostoma decandrum* (Roxb.) Wall. ex Endl. Gen. 331. 1837.

Nectandra decandra Roxb. Hort. Beng. 90. 1814 (TYPE: *Roxburgh s.n.*!);
Fl. Ind. 2: 425. 1832.

Linostoma decandrum (Roxb.) Wall. Cat. n. 4203. 1831, sine descript.

Subscandent to scandent shrubs or lianas (?) to 15 m. tall; young stems terete, dark reddish brown, glabrous except for a few short trichomes in the leaf axils, the lenticels round, becoming horizontally elongate; axillary branches normal or rarely modified and unciform, the unciform branches usually conspicuously swollen basally. Leaf blade lanceolate or elliptic to oblong-elliptic, 3.5–10 cm. long, 1.5–3.5 cm. broad, acute or acuminate to subcaudate at the apex, cuneate to obtuse at the base, thick-coriaceous, glabrous, darker above than beneath, the costa immersed above, elevated beneath, the primary lateral veins many, inconspicuous, parallel and more or less straight, the submarginal vein well developed, almost coinciding with the margin; petiole canaliculate, rugose, glabrous, 3–5 mm. long. Inflorescences borne terminally on the young shoots, generally involving several nodes, often compound; each inflorescence 3–7(–12)-flowered, subracemiform to rarely umbelliform, glabrous, the primary peduncle 2.7–5.5 cm. long, often with the reduced leaf of the subtending node near the base, the rachis 1–5 mm. long, the secondary peduncles 2–7 mm. long, often distally dilated, the bracts opposite or subopposite, borne at the middle of the primary peduncle or below, ovate, elliptic or oblong-elliptic, 2.5–4.5 cm. long, 1–2 cm. broad, obtuse to acute at the apex, truncate to rounded at the base, almost membranaceous, glabrous, creamy white, venation much more lax than that of the leaves,



MAP I. Distribution of the species of *Linostoma*: dots, *L. decandrum*; triangles, *L. persimile*; squares, *L. pauciflorum*.

subsessile, the bracteole borne at the summit of the primary peduncle, narrowly linear, 0.3–1 cm. long, caducous. Calyx tube fusiform, 5–7(–13) mm. long, 2–2.5 mm. in diameter at the orifice, glabrous and reddish without, villous and white within but often glabrous in the lower half, the trichomes protruding from the orifice; calyx lobes linguiform, 6.5–8.5 mm. long, 2–2.5 mm. broad, as long as or longer than the calyx tube, glabrous, strongly reflexed; petals inserted at the orifice, clavate, erect, fleshy, exserted, 3.5–6 mm. long, apex irregular, their bases connate by means of an obscure annulus; stamens exserted beyond the petals, inserted in a single whorl immediately below the petals, the filaments filiform, glabrous, the antisealous filaments 6.5–9 mm. long and slightly longer than the alternisealous ones, the alternisealous filaments 4–8 mm. long, the anthers oblong, about 1 mm. long, 0.75 mm. broad, the connective basally inflated but not produced beyond the pollen sacs, the pollen sacs appearing confluent and hippocrepiform following anthesis; disc of small, irregularly shaped lobes, more or less adnate to the calyx tube, less than 0.5 mm. tall, each lobe glabrous or more often bearing a number of short trichomes; stipe and ovary ellipsoid, about 3 mm. tall, densely sericeous, the style filiform, 8–11 mm. long, sericeous at the base, otherwise glabrous, the stigma mammiform, exserted beyond the anthers, about 0.75 mm. in diameter; pedicel 3–4.5 mm. long, glabrous. Fruit (immature?) ovoid, 8–12 mm. long, 4–8 mm. in diameter, sericeous, dull red, the longitudinally and unilaterally ruptured calyx tube more or less persistent at the base; pedicel 5–7 mm. long, somewhat swollen.

ILLUSTRATIONS. Denkschr. Bot. Ges. Regensburg 3: *t.* 7. 1841; Bailon, Hist. Pl. 6: 104. *figs.* 72, 73. 1877; Pflanzenfam. III. 6a: 232. *fig.* 82. *A–E.* 1894; Lecomte, Fl. Gen. Indo-Chine 5: 173. *fig.* 16. 1915; Bibl. Bot. 27(111): *t.* 2, *fig.* 11. 1934.

DISTRIBUTION. Eastern India, East Pakistan, Burma, Thailand, Vietnam, Laos, and Cambodia, the plants associated with evergreen scrub or forests, collected at altitudes up to 200 meters. Flowering specimens collected in January, April, June, November and December, specimens in fruit collected in December and February. Roxburgh (Fl. Ind. 2: 425. 1832) says that the plants flower in October and the seeds ripen in January, February and March.

India. WEST BENGAL: Calcutta, (cultivated?), *Gaudichaud* 324 (GH). MANIPUR: Piphima, *Meebold* 5164 (G). ASSAM: Sialsuk, Lushai Hills, *Parry* 410 (K). East Pakistan. EAST BENGAL: Sylhet, *Wallich* 4203 (BM, G, L, M), *Roxburgh* "1813" (BM, G), "1830" (K), without collector, (G, L, W); Chittagong Division, *Cowan s.n.* (US); Chittagong Hills, *Dr. King's collector* 106 (US), 220 (G, L), *Hooker & Thomson s.n.* (BM, G, GH, K, L, M, P, U, W). Burma. KACHIN: Myitkyina District, Tagwin, *Parkinson* 316 (K); Myitkyina District, hills w. of Hopin, *Parkinson* 347 (K); Bhamo, *Cubitt* 1047 (A). Thailand. CHONBURI: Chonburi, on trail between Mapkhla and Thapsai, *Smitinand* 3637 (L); Khow Diu near Sriracha, *Collins A* (BM), 1797 (BM, US). NAKON RATCHASIMA: Hui Reng, Kerat (Korat), *Kerr* 17588 (BM); Kao Lem, Korat, *Put* 3573 (BM). RAYONG: Ban Pe, Rayawng (Rayong), *Put* 2763 (BM). Vietnam.

ANNAM: Nha Trang, *Alleizette s.n.* (L); Tourane, *Clemens & Clemens* 3465 (P); Col de Braian, Pnom-sapoum, by Blao, *Poilane* 23698 (K). Laos. CHAMPASSAK: Bassac, *Thorel* 2612 (P). Cambodia. Insula Phu Quoc, *Pierre* 1470 (P), 19794 (BM). Without Locality. *Wallich* 2247 (C), *Bruce s.n.* (W).

There has been considerable confusion and error as to the proper citation of authorship of the genus and of this, the type species. The generic name was first used by Wallich in 1831 (Cat. n. 4203); this publication consists of the name *Linostoma decandrum* and the citation "Hort. Beng." From this scrap of information it is evident that Wallich intended a "new combination" based on *Nectandra decandra* Roxburgh (Hort. Beng. 90. 1814). Roxburgh included here, in addition to the epithet, the common name, the place of collection, a two-symbol description and the time of flowering. It was not until Endlicher in 1837 (Gen. 331) published a Latin diagnosis for *Linostoma* that either the genus or Wallich's "combination" became valid. The citation of the type species thus should be *Linostoma decandrum* (Roxburgh) Wallich ex Endlicher.

As a result of Roxburgh's publication (1814) he is given credit or rather discredit for an illegitimate genus (*Nectandra* Roxb. non alior) which is usually cited in the generic synonymy. However, in a subsequent publication (Fl. Ind. 2: 425. 1832) he maintains (despite Wallich's combination of which he probably was not aware) the name *Nectandra decandra*, furnishes generic and specific descriptions and attributes the genus to Jussieu! Indeed, Jussieu, in an earlier work (Gen. Pl. 86. 1791), had published an account of the genus *Nectandra* which was based, in turn, on *Nectandra* Berg. and which included a generic description and a single species based on *Gnidia sericea* L. The illegitimate genus *Nectandra* Berg. (Descript. Pl. Cap. 131. 1767) is composed of three previously described 4-merous species which are not congeneric with our 5-merous *Linostoma decandrum*. Thus Roxburgh did not describe a new genus but merely expanded the concept of a previously existing one. That he was in error is of little consequence. Since the citation in generic synonymy of all genera in which species of a particular genus have been misplaced leads to absurdity, these misplacements are adequately and properly cited within the specific synonymy.

There is additional confusion concerning the type specimen. To the best of my knowledge a type has never been selected, although most authors in discussing this species include the citation of *Wallich* 4203. As a result of examining a number of specimens, all labeled *Wallich* 4203, I have come to the conclusion that these collections are a heterogeneous group. Four I believe to be authentic Wallich collections: Munich with a penciled label "4203," probably written by Wallich; Leiden with a penciled "4203"; British Museum with the penciled label "4203, Wallich Nov. 1829," also probably written by Wallich; and finally a Geneva specimen with a printed label "Wallich 1829." There are a number of other specimens which may also be Wallich collections, for they bear the "Catalogue" number, but I suspect that these specimens were either collected after the publication of the "Catalogue" or that the number was added

to earlier collections as a means of specific identification, regardless of the collector. Some examples are specimens at Leiden and Geneva which bear the "Catalogue" number, but lack collection data, and a specimen from Kew which bears the "Catalogue" number, but the date 1830. There is also a collection at Vienna which bears a printed label upon which in red ink the "Catalogue" number, epithets, place of collection and collector (H. Bruce) have been added. Therefore, it seems that considerable caution must be used in evaluating specimens bearing the "Catalogue" number. However, in spite of past inference, the Wallich collections do not contain the type among them! The type must be selected from the collections of Roxburgh made prior to 1814. I have seen two specimens which probably qualify: one from the Geneva herbarium with a handwritten label, "Nectandra decandra Roxb., Ex Sylhet montibus," and, on the same label and written at a later date in another hand, "Linostoma dicandrum. Wallich"; a second specimen from the British Museum bears a label written in ink, almost certainly by Roxburgh, "Nectandra decandra probably a *Dais*, or in all events a *Thymeleae*." Added below in pencil is the notation "Roxburgh 1813." Inasmuch as the British Museum specimen appears to be best qualified I select it as the lectotype. It is composed of two flowering branchlets and a packet containing inflorescences, flowers and very immature fruit.

2. *Linostoma persimile* Craib, Kew Bull. 1911: 452. 1911 (TYPE: *Kerr 814!*).

Shrubs to 1.5 m. tall; young stems slender, terete, light brown to reddish brown, glabrous, the lenticels inconspicuous; axillary branches normal or sometimes slightly recurved. Leaf blades rotund, broadly elliptic to obovate, 2–3 cm. long, (0.8–)1–2.5 cm. broad, mucronulate and obtuse, truncate, or retuse at the apex, cuneate at the base, thin-coriaceous, glabrous, darker above than beneath, the costa immersed above, elevated beneath, the primary lateral veins many, parallel and more or less straight, the submarginal vein inconspicuous, almost coinciding with the margin; petiole shallowly canaliculate, slightly rugose, glabrous, 1–2 mm. long. Inflorescence borne terminally on the young shoots, involving a few to several nodes, sometimes compound; each inflorescence 3–6-flowered, umbelliform, glabrous, the primary peduncle 2–4 cm. long, often bearing the reduced leaf of the subtending node near the base, the rachis about 1 mm. long, the secondary peduncles at most 0.5 mm. long, distally dilated, the bracts subopposite, borne at the middle of the primary peduncle or below, ovate to elliptic, 2–3 cm. long, 1–2 cm. broad, acute and mucronulate at the apex, obtuse to subcordate at the base, membranaceous, glabrous, with a venation more lax than that of the foliage leaves, the bracteole borne at the summit of the primary peduncle, linear, about 1 mm. long, caducous. Calyx tube tubular, 8–10 mm. long, 2–3.5 mm. in diameter at the orifice, glabrous without, glabrous within, yellow; calyx lobes linguiform, 4–4.5 mm. long, 1.5–2.5 mm. broad, much shorter than the calyx tube, glabrous, erect or slightly spreading; petals inserted

at the orifice, liguliform, erect, exserted beyond the anthers and the stigma, 3–3.5 mm. long, gradually tapering to the acute apex, fleshy; stamens inserted in two distinct whorls, the filaments filiform, glabrous, the anti-sepalous filaments about 1 mm. long, the alternisepalous filaments to 0.5 mm. long, the anthers oblong, 0.75–1 mm. long, 0.5 mm. broad, the connective obtusely produced beyond the pollen sacs, the upper antisepalous filaments inserted just below the petals, exserted, the lower alternisepalous filaments inserted about an anther's length below the anti-sepalous ones, included; disc of minute irregular lobes, adnate to the calyx tube, glabrous; stipe and ovary ellipsoid, about 2 mm. long, 0.75 mm. in diameter, densely sericeous, the style filiform, 6–7.5 mm. long, glabrous, the stigma capitate, exserted beyond the stamens; pedicel 1.5–3 mm. long. Fruit accrescent, surrounded by the persistent calyx, the calyx more or less narrowly lageniform, 11–13 mm. long, 5–7 mm. in diameter, the lobes erect, the drupe broadly fusiform, 7–9 mm. long, 6–7 mm. in diameter, sericeous at least towards the apex; pedicel slightly swollen.

DISTRIBUTION. Burma and Thailand. Collected at altitudes of from less than 50 meters to 1650 meters. Found in deciduous forest or open "pine jungle." The collections indicate flowering in September, November, and December, with fruiting known in November and December.

Burma. KARENNI: Karen Country and Hills, *Kurz 990* (M). **Thailand.** CHIENGMAI: Camp Hoi Chan Kiang, Doi Sootep, *Rock 123* (US); summit of Doi Chom Cheng, Doi Sootep, *Rock 1173* (US); Doi Sootep, *Garrett 1397* (A, L, US), *1436* (K, L), *Kerr 814* (K-holotype, BM), *s.n.* (BM). **Without precise locality:** Tung Quang, Petchabuni (?), *Kerr 20584* (BM), *Marian 2759* (K).

The collections *Kerr 20584* and *Marian 2759* have not been mapped for I am not certain of the spelling of the locality on the handwritten labels, which read either "Petchabuni" or "Petchaburi." Since a distance of about 250 miles separates these two cities, it seems best not to make a judgment at this time. If an itinerary of Kerr's travels exists, the location could probably be determined.

The holotype has with it a packet containing a rather unusual flower. This flower, which is nearly mature, has two petals (both lateral with respect to the single calyx lobe which they flank) which have become connate below by their lateral margins. In addition, these fused petals have produced a smaller subsidiary petal between them. The stamen standing in front of this petalaceous anomaly is unusual in that the filament is almost hispid, in striking contrast to the glabrous filaments of the remaining nine stamens. The position of the stamen, i.e., standing within this petalaceous anomaly, provides evidence by its gross morphological position, of the true petalaceous nature of this structure.

A number of flowers in several collections display an included stigma. Close examination indicated that the elongation of the style is delayed until after the pollen is shed. I assumed that this might be some form of mechanism for the prevention of self-pollination, specifically, proterandry. However, Burrows (1960) has described a somewhat comparable

mechanism in the genus *Pimelea* and his observations and conclusions may be applicable to this species. In essence, he found that in bisexual flowers early pollination inhibited elongation of the style, with the result that fertilization may take place and the style remained included, late pollination inhibited elongation to a lesser degree, even though fertilization could no longer occur, and, finally, the lack of pollination allowed the style to elongate greatly and thus the stigma to become well exserted.

3. *Linostoma pauciflorum* Griffith, Calcutta Jour. Nat. Hist. 4: 234. 1844 (TYPE: *Griffith 4376!*).

Linostoma leucodipterum Hallier f. Med. Rijksherb. 44: 28. 1922 (TYPE: *Hallier f. B.2261!*).

Linostoma longiflorum Hallier f. *ibid.* 29 (TYPE: *Haviland 1759!*).

Shrubs, trees, or climbers, to 25 m. tall; young stems filiform to slender, terete, light to dark brown, glabrous except for a tuft of short trichomes in the leaf axils, the lenticels inconspicuous; axillary branches normal or gently to strongly uncinat, becoming swollen at the base. Leaf blade ovate, lanceolate, narrowly to broadly elliptic or oblong-elliptic, 1–5 cm. long, 0.5–2.5 cm. broad, mucronate and acute, obtuse, truncate or retuse at the apex, cuneate to obtuse at the base, thin-coriaceous, glabrous, but sometimes appearing farinose beneath, darker above than beneath, the costa plane to immersed above, plane to elevated beneath, the primary lateral veins numerous, more or less straight and parallel, inconspicuous, the submarginal vein well developed, coinciding with the margin; petiole canaliculate (although sometimes scarcely so), 1–3 mm. long, rugose, glabrous. Inflorescences borne from the axils of the terminal portions of the young stems, simple or compound, glabrous except for occasional trichomes near the summit of the primary peduncle; each inflorescence 1–5-flowered, umbelliform, the primary peduncle 2–18(–30) mm. long, often with the reduced leaf of the subtending node near the base, the rachis to 0.5 mm. long, the secondary peduncles obsolete, to 0.5 mm. long, somewhat dilated distally, the bracts borne from the middle to the summit of the primary peduncle, opposite, subopposite, or alternate, foliaceous or reduced and bracteolate, linear, lanceolate, ovate, elliptic or oblanceolate, 2–35 mm. long, 2–18 mm. broad, mucronulate and acute, obtuse, or truncate at the apex, acute, obtuse, or subcordate at the base, membranaceous, glabrous, white, the venation more lax than that of the foliage leaves, the bracteole borne at the summit of the primary peduncle, linear, to 10 mm. long, sometimes caducous, or extremely reduced and represented by a small lump of tissue in the axil of which stand a few trichomes. Calyx tube tubular to ellipsoid, 7–25 mm. long, about 0.5 mm. in diameter at the orifice, glabrous and green to white without, glabrous or partially to completely villous within, a few trichomes exserted beyond the orifice; calyx lobes lanceolate or elliptic to oblanceolate, 3–12 mm. long, 1.5–3 mm. broad, usually glabrous, spreading; petals inserted at the orifice, narrowly clavate,

fleshy, exserted, erect, 5.5–7.5 mm. long, obtuse to irregular at the apex, glabrous; stamens inserted in two close whorls just below the petals, exserted beyond the petals, the filaments filiform but enlarging distally, 4.5–10 mm. long, glabrous, the antisepalous filaments somewhat longer than the alternisepalous ones, the anthers more or less oblong, 0.5–1 mm. long, 0.5–0.75 mm. broad, the connective enlarged so as to displace the pollen sacs to its lateral margins but not produced beyond the pollen sacs; disc annular, with irregular lobes, 0.25–0.5 mm. high, glabrous; ovary and stipe oblong-obovoid or obovoid, 3–7.5 mm. long, sparsely to densely sericeous, the style filiform, 6–20 mm. long, glabrous or with occasional trichomes, the stigma capitate, exserted beyond the stamens; pedicel 5–8 mm. long. Calyx tube accrescent in fruit, ellipsoid but tapered more sharply above than below, 12–15 mm. long, 6–7 mm. in diameter, the drupe ovoid.

ILLUSTRATION. *Flora Malesiana* I. 6: 26. fig. 11. 1960 (as *L. longiflorum* and *L. pauciflorum*).

DISTRIBUTION. Thailand, south to Singapore and east to Borneo; collected from sea level to 200 meters. Flowering in March, April, June, August, September, and October; collected in fruit in December. Found in evergreen scrub, wastelands, and primary peat forests; the Hillard collection is from "undergrowth on rubber estate."

According to Kerr the root is sometimes used for poisoning fish.

Thailand. PATTANI: Yala, *Kerr* 7258 (BM); Kok Po, *Kerr* 15073 (BM). SONGKHLA: Hat Zai, *Kerr* 13667 (BM). SURATTHANI: Surat, *Kerr* 11302 (BM), *Kerr* 11820A (BM). LOCALITY UNCERTAIN: Tako, Qungsuam (?), *Kerr* 11870 (BM). **Malaya.** KEDAH: Langkawi Islands, *Curtis s.n.* (P), *Hillard* KL1411 (A); Langkawi, Palo Lingsong (?), *Curtis*, 1890 (BM). PERAK: Pangkore Island, *Scortechini* 983 (K), *Burkill & Shah* HMB 240 (K, L). PERLIS: Chapnema (?), *Ridley* 14916 (BM). YALA: Pulau Penang, Telok Bahang, Toi, 1905 (BM), *Sinclair* SFN 39304 (L). WITHOUT LOCALITY: *Maingay* 1308/3 (L). **Singapore.** *Griffith* 4376 (K-holotype of *L. pauciflorum*); Changi, *Ridley* 1858 (BM); Botanic Gardens, *Kiah* SFN 37931 (BM, L). **Sarawak.** Kuching, *Haviland* 1759, Oct. 1892 (L-holotype of *L. longiflorum*; BM, GH, K), *Brooke* 9696 (G, L); Binatang, *J.A.R. Anderson* 9047 (L); Tanjong Po, *Brooke* 10603 (G); near Long Kapa, Mount Dulit (Ulu Tinjar), *Richards* 1312 (A, K). **British North Borneo.** Sandakan and vicinity, *Ramos* 1799 (A, US); Gaya Island, *Haviland* 1440 (K). **Borneo.** W. BORNEO: zwischen Súngai Dějmělá und Gúnŋg K(e)lamm, *Hallier* B.2261 (isotypes of *L. leucodipterum*, L, P).

My treatment of this group of specimens as a single species requires more than a perfunctory explanation because of the recent work of Hou (1960) for the *Flora Malesiana* in which the treatment differs. Geographically, the specimens can be divided into two groups, one restricted to the island of Borneo and the other to peninsular Malaya. I shall discuss the relationship of the Bornean specimens to each other and to peninsular specimens (when of some significance).

Hou (1960) has recognized two species from Borneo, *Linostoma pauciflorum* and *L. longiflorum*. His key to these species is based upon differ-

ences in the bracts, particularly the size and the degree to which they cover the lower half of the calyx tube, as well as the length of the calyx tube. On the basis of his key I have seen two collections which clearly can be placed with *L. longiflorum*; they are *Haviland 1759* (type of *L. longiflorum*) and *Anderson 9047*. In addition, *Jahri 166* may belong with this unit, but the Leiden specimen examined lacks inflorescences. It has been annotated by Hou as *L. longiflorum*, and he may have seen a more complete specimen from the Bogor herbarium.

The leaves of the two "species" are extremely variable in shape and size, although the leaves of *Haviland 1759* tend to be the broadest of all Bornean collections (but no broader than those found on some of the peninsular specimens). There appears to be no certain way to separate two species on the basis of either leaf shape or size.

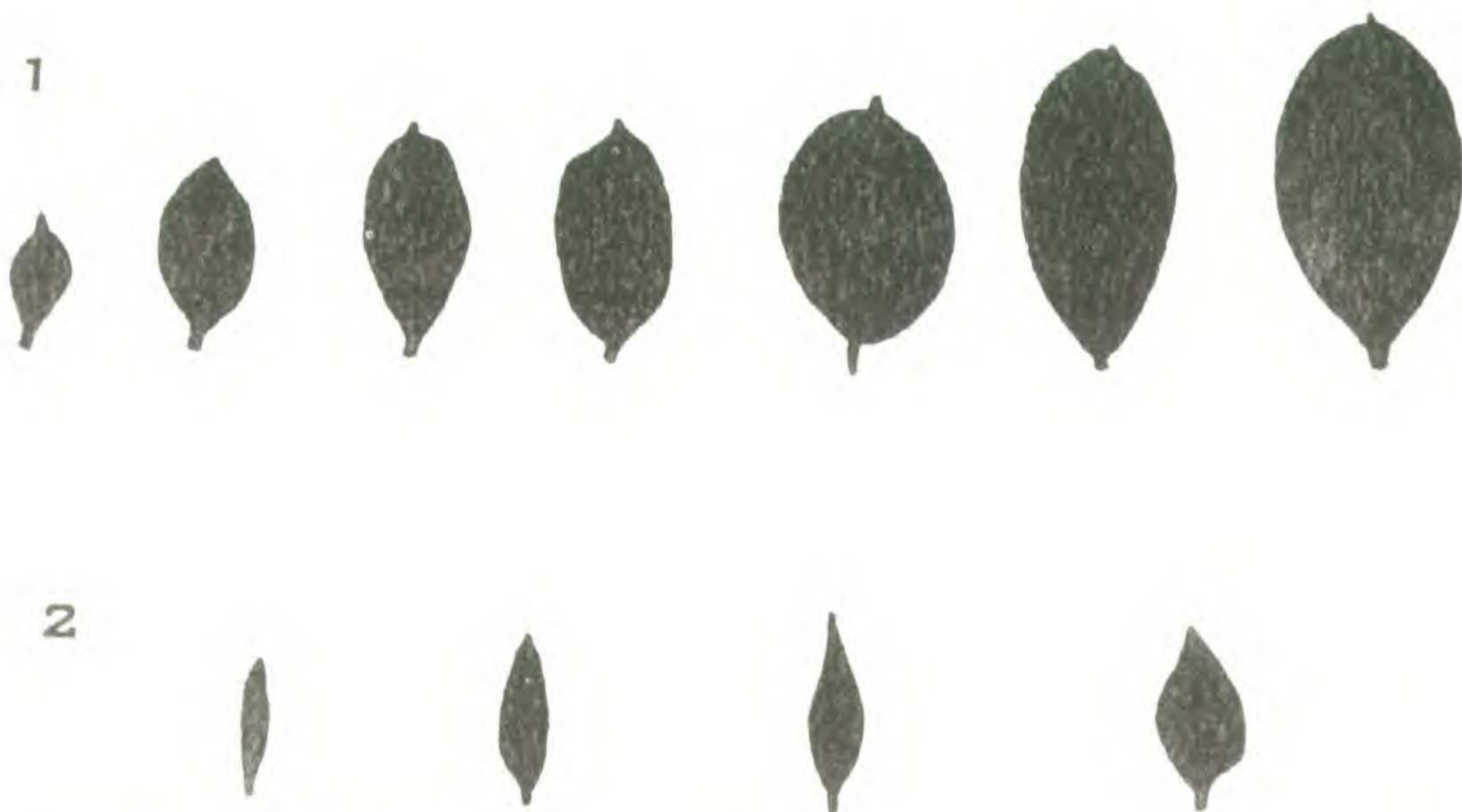
As already indicated in the introductory comments, the structure of the leaf is rather constant throughout the genus, but several characteristics in this connection are of interest. The stomata of this species are similar to those of *Linostoma persimile* but quite different from those of *L. decandrum*. The lower leaf surface often appears farinose under magnification. This phenomenon is due to the papillate shape of the outer periclinal wall of individual cells of the lower epidermis. This condition can be demonstrated to a greater or lesser degree in most of the collections, either peninsular or insular and including the type of *L. longiflorum*, but is not found elsewhere in the genus. Finally, it must be mentioned that Hallier in the original description of *L. longiflorum* made reference to a fungal infection in the type. It was thus a surprise to find the leaves of *Anderson 9047* similarly affected. None of the Bornean collections referable to *L. pauciflorum* (by Hou's system) appears, on the basis of cleared leaves, to be infected, and to draw a conclusion is almost irresistible.

The basic structure and size of the inflorescence is essentially the same in both "species," although there are certain differences which require discussion. In *Linostoma longiflorum* the number of flowers per inflorescence is one, whereas in *L. pauciflorum* it is rarely one, generally two (Borneo), and sometimes as many as five (peninsular). There does not seem to be any real correlation between the number of flowers per inflorescence and their size as one might expect to find.

The position of the bracts near the summit of the primary peduncle is the same in all Bornean specimens. In the peninsular specimens, in which the bracts are alternate, one of the pair is borne at the summit of the primary peduncle. This distal position of the bracts gains importance because it is unique within the genus (other species having the bracts borne at the middle of the primary peduncle or below).

The importance of the bracts themselves is magnified by their use as a "key" character. In *Linostoma longiflorum* the bracts vary in length from 2–12 mm. and their shape is usually linear or linear-lanceolate. The bracts of specimens referable to this species which I have cleared seem to have a poorly differentiated vascular system, perhaps an indication that growth of the bract had ceased before attainment of "mature" form. The

bracteole, in contrast, is well developed. In *L. pauciflorum* the bracts vary from 8–35 mm. in length, and the shape, although variable, is considerably broader than that found in *L. longiflorum*. The bracteole, in contrast, is poorly developed and is sometimes reduced to only a small lump of tissue in the axil of which stands a tuft of trichomes. It is tempting to consider a type of developmental anomaly which indiscriminately “stunts” the growth of the bracts (*L. longiflorum*) on the one hand and growth of the bracteole (*L. pauciflorum*) on the other.



TEXT FIG. IV. Variation in bract size and shape in two collections of *Linostoma pauciflorum*: 1, Hallier B.2261, from Borneo; 2, Haviland 1759, from Sarawak (Natural size).

Outlines of a series of bracts showing extremes in variation from two collections representing *Linostoma longiflorum* (Haviland 1759) and *L. pauciflorum* (Hallier B.2261) are presented in TEXT FIG. IV. It is of more than casual interest that a size overlap occurs and that the largest bract in the Haviland collection is quite similar in shape to the smallest bract found in the Hallier collection. Additional collections from Borneo will be necessary before this problem of size variation and overlap can be evaluated. It should be obvious at this point that the degree to which the bracts cover the base of the calyx tube is determined by the length of the bracts. This does not mean that the key does not work in the area of overlap. There are generally enough bracts on the available specimens to indicate strikingly to which “species” the specimen belongs, but I think that it does detract from the validity of this key character.

Generally speaking, the vegetative portions of a plant may be expected to be more variable than reproductive structures. To check this generality a study of morphological and, to a lesser degree, anatomical characteristics of the flower was made. As in the case of the leaves, the sample is extremely small, but the floral characteristics showed a striking homo-

geneity which cannot be easily dismissed. The calyx tube is the same shape and has the same type of pubescence in all Bornean collections. In flowers of insular specimens the calyx tube is variously villous within and is in sharp contrast to those of the peninsula in which the calyx tube is glabrous within. This difference is not considered taxonomically significant. The length of the calyx tube (a key character) is variable but it does not have a comparable overlap as found in bract size. In *Linostoma pauciflorum* it varies from 13–15 mm. in length (insular) and from 7–15 mm. in length (peninsular), whereas in *L. longiflorum* it varies from 17–25 mm. in length. Tube measurements must be taken from flowers at anthesis as there is considerable elongation of the tube immediately prior to anthesis. The occasional oblanceolate shape of the calyx lobes is a character shared by both “species” and is unique within the genus. The margin of the calyx lobe is sometimes furnished with a few very small trichomes in *L. pauciflorum* (both insular and peninsular) but I have not seen them in the two collections referable to *L. longiflorum*.

The petals of the two are alike in shape, size, insertion, and degree of exsertion. Indeed, in the original description of *Linostoma longiflorum* Hallier says of petals and stamens, “fere ut in sp. praecedente” (*L. leucodipterum*,* synonymous with *L. pauciflorum*). The most striking point is that the petals are vascularized by a single vascular strand, a condition that is once again unique within the genus (the other species lacking vascularization of the petals altogether).

Similarities within the androecium are also to be found as indicated by Hallier’s original description of *Linostoma longiflorum*. The insertion of the stamens and their relative exsertion is the same in all specimens. The peculiar swelling of the filament towards its summit is common, as is the very expanded connective. (The connective is enlarged to the extent that the pollen sacs are displaced to its lateral margins and one wonders whether or not the dehiscence can be spoken of any longer as introrse.) Examination of the pollen shows similar size and sculpturing of the exine (which is, however, rather constant throughout the genus). The disc is the same type in all specimens.

The gynoecium is notable for the very long stipe (longest in the genus) which gradually tapers into the ovary. The pubescence of the stipe and ovary is similar and differs from other species in that the trichomes tend to be shorter and blunter. However, it is in the vascularization of the ovary that the soundest factual homogeneity is found. That is not to say there is no variation in the specimens of this species, for there certainly is, but it is the kind of variation that is indicative of a basic relationship. A series of camera lucida drawings made from cleared and stained ovaries from *Ridley 1858* (representative of peninsular *L. pauciflorum*), *Hallier B.2261* (isotype of *L. leucodipterum*) and *Haviland 1759* (isotype of *L. longiflorum*) is presented in TEXT FIG. III, 3–5. In all three examples a well-developed ovular trace is present, in contrast to the very poorly developed or obsolete (?) ovular trace of other species

* Holotype deposited at Bogor and not seen by me, isotypes at Leiden and Paris.

(see TEXT FIG. III, 1, 2). In addition, the number of accessory traces is notably decreased and a trend of reduction within the series itself seems a remote possibility.

In summation, the combination of shared morphological and anatomical characteristics which are often unique within the genus is overwhelming evidence of the conspecific nature of this group. In addition, I think that the dissimilarities noted, which are of a quantitative and not a qualitative type, fall within the range of variation that could be expected within a single species of this family.

STATUS UNDETERMINED

Psilaea Miquel, Fl. Ind. Bat. Suppl. 355. 1860 (TYPE: *P. dalbergioides*).

Psilaea dalbergioides Miquel, *ibid.* (TYPE: *Teysmann*?).

This genus and species were based by Miquel on a Teymann collection from Siboga [sic, Sibolga], Sumatra. Presumably the specimen would be deposited in the herbarium at Utrecht but no record can be found of it there at present.

Kurz (1870, p. 82, 83) in a discussion following the description of *Linostoma siamense* says that he has authentic specimens of the type species (*Psilaea dalbergioides*) and "cannot see how the species should differ from *Linostoma pauciflorum*, Griff." From his short discussion two important conclusions can be drawn: (1) that Kurz did not distinguish between *Linostoma* and *Enkleia*; (2) that he had an authentic specimen during his curatorship at the Royal Botanic Gardens, Calcutta. I have not yet determined whether this specimen is extant at Calcutta.

This species has been referred repeatedly to the synonymy of *Linostoma pauciflorum*. I feel that this action is the result of Kurz's comments, and that it involved no subsequent investigation. Inasmuch as Kurz did not distinguish between *Linostoma* and *Enkleia* I prefer to defer a decision regarding this name until the type is located or authentic specimens from Sumatra may be examined. I have not seen any specimens from Sumatra referable to the genus *Linostoma* to date, although Hou (1960) gives Simalur as a locality for *L. pauciflorum*.

Linostoma sect. **Psilaea** (Miq.) Hallier f. Med. Rijksherb. no. 44, 28. 1922.

Hans Hallier (1922) when treating the genus *Linostoma* split it into two sections: *Eulinostoma* Meissner, including only *L. decandrum*, and *Psilaea*, presumably based on Miquel's *Psilaea dalbergioides* as indicated by parenthetical credit, including Hallier's two new species *L. leucodipterum* and *L. longiflorum*. Although his brief descriptions would fail to hold today and infrageneric categories, with the exception of species, are considered unnecessary in view of the small number of species, his concept was in essence correct. *Linostoma decandrum*, on the basis of several

morphological characteristics, stands isolated from *L. persimile* and *L. pauciflorum*.

Linostoma incertae sedis

A collection from Brunei, *Ashton BRUN 573*, has caused me considerable concern. It is an immature flowering specimen which is somewhat abnormal due to a fungal infection. The original identification was "*Linostoma leucodipterum* Hall. f.," subsequently modified to "*Linostoma pauciflorum* Griff." by Hou (annotation, 1958, and Identification Lists of Malaysian Specimens, July, 1960). Superficially it does resemble this species, but closer examination shows some differences, such as general pubescence, position of the inflorescence, number of flowers per inflorescence, lack of a disc, and pubescence and shape of the ovary. I should not be surprised to find that it represents an undescribed species but believe that any taxonomic designation at this time would be premature. I have, however, taken the liberty of including here a description which the reader will appreciate as being lacking in many respects.

Climber to 25 m. tall; young stems generally slender, terete, ferruginously tomentulose and glabrescent, the lenticels inconspicuous; axillary branches normal. Leaf blades ovate to lanceolate, 2–4.5 cm. long, 1–2 cm. broad, acute to obtuse at the apex, cuneate to obtuse at the base, chartaceous, glabrous, except for occasional trichomes beneath, darker above than below, the costa immersed above, elevated beneath, the primary lateral veins many, parallel and more or less straight, the submarginal vein well developed, coinciding with the margin; petiole canaliculate, sparsely tomentose, 1–3 mm. long. Inflorescences simple, borne terminally on the young stems or axillary branches, (5–) 10–16-flowered, sparsely tomentose, the primary peduncle 2–3 cm. long, the rachis 1–2 mm. long, the secondary peduncles about 0.5 mm. long, the bracts (with fungal infection) borne below the middle of the primary peduncle, opposite or subopposite, narrowly elliptic, 2–3 cm. long, 0.5–1 cm. broad, obtuse at the apex, cuneate at the base, membranaceous, sparsely puberulent both surfaces, the bracteole borne at the summit of the primary peduncle, linear, 0.5–2 mm. long. Immature flowers: calyx tube short-tubular, 1–3.5 mm. long, 0.5–1.5 mm. in diameter at the orifice, sparsely strigose without, glabrous within, cream-colored; calyx lobes ovate, 1 mm. long and broad, erect, glabrous within; petals inserted at the orifice, linguiform, 1–2 mm. long, ca. 0.75 mm. broad, acute at the apex, glabrous, exserted beyond the stamens; stamens borne in 2 whorls, the antisepalous whorl inserted just below the petals, exserted, the alternisepalous whorl about an anther's length below the antisepalous whorl, included, the filaments 0.5–0.75 mm. long, glabrous, the anthers oblong, to 0.5 mm. long and broad; disc absent; ovary ovoid, ca. 1 mm. tall, densely hirsute, style and stigma poorly differentiated; pedicel to 4 mm. long.

Brunei. Collected in September in primary forest, altitude 50 meters, Andulau F. R., *Ashton BRUN 573* (L).

EXCLUDED TAXA

- LINOSTOMA subg. LINOSTOMA Kurz, Jour. As. Soc. Bengal 39(2): 83. 1870, as to species cited. = *Enkleia* Griff.
- LINOSTOMA sect. LOPHOSTOMA Meissn. in Mart. Fl. Bras. 5(1): 72. 1855 (Type: *L. calophylloides* Meissn.) = *Lophostoma* Meissn.
- LINOSTOMA ALBIFOLIUM Rodr. Vellozia 1885-88. ed. 2. 67. t. 20. 1891 = *Lophostoma albifolium* (Rodr.) Gilg in Engl. & Prantl Nat. Pflanzenfam. III. 6a: 232. 1894.
- LINOSTOMA ANDAMANICA Hutchinson ex C. E. Parkinson, Forest Flora Andaman Isl. 2291. 1923 = *Enkleia* sp.
- LINOSTOMA CALOPHYLLOIDES Meissn. in Mart. Fl. Bras. 5(1): 72. 1855 = *Lophostoma calophylloides* (Meissn.) Meissn. in DC. Prodr. 14: 600. 1857.
- LINOSTOMA DINIZII (Huber ex Ducke) Lemee, Fl. Guyan. Fr. 3: 108. 1953 = *Lophostoma dinizii* Huber ex Ducke, Arch. Jard. Bot. Rio de Janeiro 1: 51. 1915.
- LINOSTOMA SCANDENS (Endl.) Kurz, Jour. As. Soc. Beng. 39(2): 83. 1870 = *Enkleia* sp.
- LINOSTOMA SCANDENS var. CAMBODIANA Lecomte, Nat. Syst. 3: 127. 1915. (Type: *Pierre 511!*) = *Enkleia* sp.
- LINOSTOMA SIAMENSE Kurz, Jour. As. Soc. Beng. 39(2): 82. 1870 (Type: *Teysmann 5986!*) = *Enkleia* sp.
- LINOSTOMA THORELII Lecomte, Not. Syst. Paris 3: 127. 1915 (Type: *Thorel 2823!*) = *Enkleia* sp.

LITERATURE CITED

- BURROWS, C. J. Studies in *Pimelea* I. The breeding system. Trans. Roy. Soc. New Zealand 88: 29-45. 1960.
- DOMKE, W. Untersuchungen über die systematische und geographische Gliederung der Thymelaeaceen. Bibliot. Bot. 27(111): 1-151. 1934.
- FOSTER, A. S. Practical Plant Anatomy. D. Van Nostrand Company, Inc. New York. 1950.
- HOU, D. Thymelaeaceae. In: Flora Malesiana I. 6: 1-48. 1960.
- KURZ, S. On some new or imperfectly known Indian plants. Jour. As. Soc. Bengal 39: 1-91. 1870.
- LEANDRI, J. Recherches Anatomiques sur les Thyméléacées. Ann. Sci. Nat. Bot. X. 12: 125-237. 1930.
- METCALFE, C. R. and L. CHALK. Anatomy of the Dicotyledons. 2 Vol. Oxford University Press. 1950.
- NEVLING, L. I., JR. A revision of the genus *Daphnopsis*. Ann. Missouri Bot. Gard. 46: 257-358. 1959.
- RIDLEY, H. N. The Dispersal of Plants Throughout the World. L. Reeve & Co., Ltd. Ashford, Kent. 1930.
- SOLEREDER, H. Systematische Anatomie der Dicotyledonen. p. 806-813. Stuttgart. 1899.